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The Reproductive System of the Army-Ant Queen, *Eciton* (*Eciton*)
Part 1. General Anatomy[1]

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INTRODUCTION

In recent contributions on colony behavior of army ants in Central America and Mexico, Schneirla (1938, 1944, *et seq.*) has shown that extensive foraging and migration probably are directly influenced by the developmental age of offspring derived from the reproductive cycle of the single queen possessed by each colony. The queen, therefore, is quite positively, though indirectly, the pacemaker of the colony. In these investigations, the close relationship between brood condition and colony behavior has been demonstrated in detail through observations and tests in field and laboratory. External evidence concerning the queen has shown that she passes through certain periodic changes. These are climaxed by the delivery of huge batches of eggs at distinct times in close conjunction with the cycle of colony events.

Schneirla's investigations (1938, 1944, 1947, 1949; Schneirla and Brown, 1950) demonstrate that a single functional queen is the sole reproductive individual through the successive brood cycles of a colony.

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[1] The three studies of which this is the first have been carried out in collaboration with the Department of Animal Behavior of the American Museum of Natural History. The writer wishes to express his thanks to Dr. T. C. Schneirla, Curator in that department, for having made available a series of queens collected and preserved by him in connection with his field investigations on army-ant behavior and biology. Each queen referred to in this study is identified by the annual series and symbol used for her colony in the original publication (Schneirla, 1947, 1949; Schneirla and Brown, 1950).

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Furthermore it is clear that her biotic potential is very great, for she deposits more than 20,000 eggs (*E. hamatum*) within a relatively short time. Moreover, she is able to maintain this phenomenal record in much the same manner at regular intervals of about 36 days.

As a matter of fact, *Eciton* queens have been exceedingly scarce in collections, for they are difficult to obtain (Wheeler, 1921, 1925). It is fortunate, therefore, that in connection with Schneirla's work, queens have been systematically captured at representative stages of the colony cycle and preserved for later study of their internal anatomy.

The next step, the study of the reproductive system of the queen, is to discover how she may discharge such enormous quantities of eggs and to find what changes occur in the system during the colony cycle. To fulfill these objectives and to present the results logically and most conveniently, the subject matter has been divided into three major topics: the general anatomy, the histology, and the oöcyte cycle of this system.

The specimens were preserved in the field as follows: three small incisions were made along each lateral line of the gaster; each specimen was immersed in Carnoy's fluid or Bouin's picro-formol solution for 24 hours or more, and then was transferred to 70 per cent alcohol for preservation. Owing, no doubt, to the superficial fat body, fixation usually varied from poor to fair and was seldom good but subsequent preservation was satisfactory.[1] The material required was dissected in the laboratory some months later and sectioned at 8 μ and 10 μ. Routine stains with haemotoxylin and eosin were generally employed. Dr. Margaret C. Tavolga very courteously sectioned the ovary of one queen ('48 PH–3, Schneirla and Brown, 1950) and used a modified Masson stain.

The specimens represented various species, mainly *E. burchelli* and *E. hamatum,* while one each were *E. rogeri* and *E. vagans*. Of these, reliance is placed on the first two (more numerous) species. It should be stated here, however, that no characteristic specific differences appeared between the reproductive organs of any of these species. The *burchelli* queen may

[1] Many of the difficulties experienced by Dr. Hagan in this investigation may be attributed to the faulty fixation of specimens. For the most part, the specimens used in his study were queens that I had kept alive in captivity for one or more days following their capture, before fixation, to carry out tests and behavior observations essential to the primary investigation. There is every reason to believe that once an *Eciton* queen has been removed from her colony under natural conditions, deleterious organic changes soon set in which lead inevitably to death unless she is returned within about five days. Such changes evidently are progressive and almost certainly account for a considerably greater resistance of the tissues to adequate fixation than with freshly captured queens.—T. C. Schneirla

possess a greater number of ovarioles or have more oöcytes in each, for her biotic potential appears to exceed the other species considered. Specific comparative counts were not made.

Only one paper seems to have appeared on the reproductive system of the army-ant queen, and this treated *E. schmitti* Emery. Holliday, in her study (1904) of some ergatogynic ants, gave a few brief observations on the above species. From her remarks and a single illustration, it is quite evident the subtemperate *E. schmitti* and the tropical species considered here vary greatly in structural details.

Eciton schmitti possesses a wide, sac-like, median oviduct and quite short, curving, paired oviducts. The latter are represented as broadly branching from the median oviduct in a shape resembling the arms of a horseshoe. Over most of the length of the paired oviduct the ovarioles, estimated at approximately 400 or 500 in number in each ovary, are multiserially arranged in origin. The above range in numbers of ovarioles was derived from a tabulation of 162 from, perhaps, a little less than half of one ovary. Each ovariole was thought to contain eight to 12 oöcytes. It was also noted that a very large spermatheca lies dorsal to the median oviduct, though this is not represented in the figure which accompanies Holliday's description.

ANATOMY OF THE ABDOMEN IN THE *ECITON* QUEEN

Before a description of the internal organs is given, a few observations on the external abdominal region should be presented. The abdomen is constricted anteriorly into a narrow petiole to join the thorax. It is expanded posteriorly into an enlarged gaster which contains the reproductive system and other abdominal organs.

THE GASTER: This portion of the abdomen of the contracted queen of these *Eciton* species shows, externally, five strongly telescoped segments during most of the nomadic phase. The sclerotized plates of tergites and sternites greatly overlap at this time. However, when the physogastric condition is attained in the early statary phase of the cycle the gaster becomes so greatly distended that the sclerotized areas are widely separated. It is then revealed that these areas are actually but a small portion of the exoskeleton. When the queen is full physogastric, the sclerotized areas appear as reddish brown, ovate, tergal plates distributed over greatly expanded cream-colored pleural and intersegmental areas. Actually, when viewed from the side, the tergal part of the gaster describes a convex arc while the sternal midline lies almost straight. Both the contracted and the

physogastric queens are shown in figure 1. After ovulation the gaster subsides quickly and shows no more sign of unsclerotized cuticle than that of the worker caste. Posteriorly an ovipositor, about 1.75 mm. long, projects slightly beyond the small visible terminal segment.

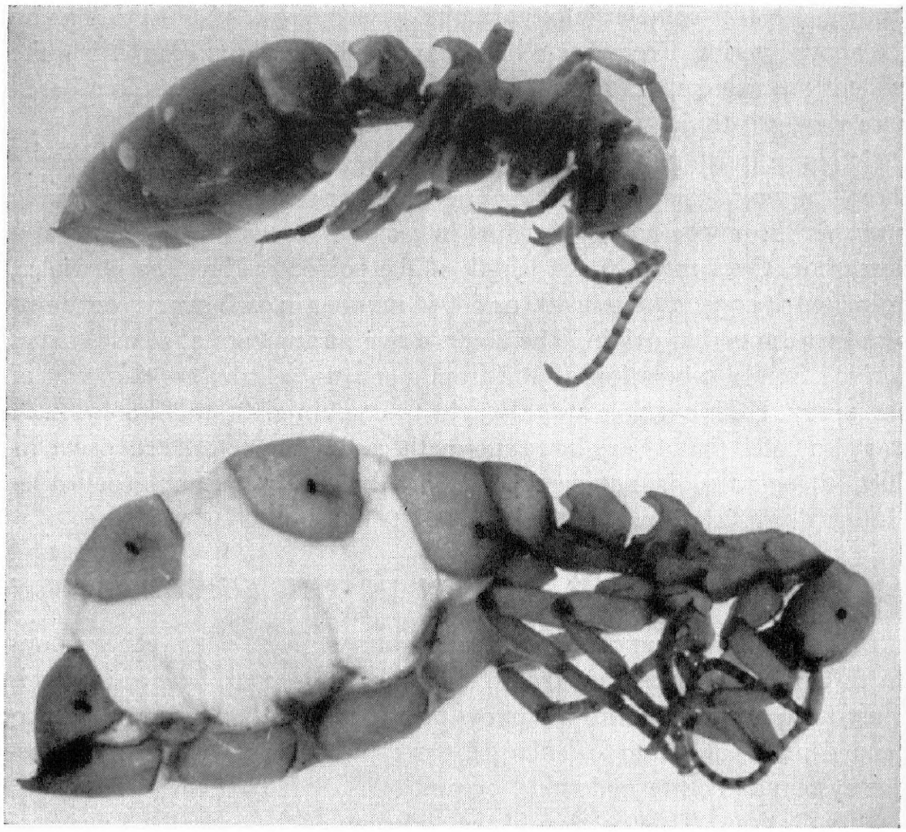

FIG. 1. Queens of *E. hamatum* in the contracted (upper) and physogastric (lower), or gravid, condition. Total length of the contracted queen, 17 mm. Photographs by Dr. Virgil Argo, Department of Biology, the City College of New York. (After Schneirla, 1944.)

Upon opening the gasters of contracted and physogastric queens by removing the dorsal exoskeleton along the margins of the pleural boundary, one can at once realize why it enlarges and diminishes periodically in size. Two factors seem to operate simultaneously to produce physogastry. One is the great accumulation of reserves in the fat body which, while present between all the organs to some extent, lies principally in the form of a sheet of tissue immediately within the somatopleural musculature. The other factor regulating the size of the gaster is the enlargement or subsi-

dence of the ovaries depending upon the developmental age of the contained oöcytes.

Under conditions normal to the nomadic phase, the *Eciton* queen is maximally contracted and regularly demonstrates great physical strength and endurance in foraging her way over a tortuous route of 300 meters or more in the nightly emigration of her colony to its new nesting site (Schneirla, 1938, 1944). In the statary phase, when the queen regularly becomes physogastric and delivers each time a huge new batch of eggs, the colony does not emigrate but remains for about 20 days at the same site. This concurrence of events undoubtedly constitutes an important adaptive fact, for when physogastric the queen could accomplish an emigration with her colony only at considerable risk, if at all. Then her widely exposed and tightly stretched intersegmental membranes, although tough, would protect her only very inadequately against shock, abrasion, and other numerous risks of the journey. Also at that time her viscera and tracheae must be abnormally compressed. This very conceivably would render her incapable of the oxygen intake essential for moving her huge bulk over the long route, at a time when her regular oxygen requirements must be excessive as compared with those in the contracted condition. A greatly increased oxygen supply must be needed for the metabolic conversion of fat reserves to yolk for the multitude of oöcytes produced in a single series. However, in the existing cyclic pattern of function in an *Eciton* colony as Schneirla has found, processes external to the queen regularly bring nomadic behavior to a halt at a specific time when the queen is still in an essentially contracted condition.

The existence of great internal pressure in the gaster of a physogastric queen is attested by the tightness with which the intersegmental membranes are stretched. A small rupture in the membrane of a living or preserved physogastric queen usually results in a marked visceral rupture. When the author first attempted to dissect the distended abdomen of a physogastric *Eciton* queen, only a small preliminary incision in the membrane along the pleural edge of a median tergite brought startling results. A release of pressure at once ruptured the ovaries and oviduct so violently that many hundreds, perhaps thousands, of mature and nearly mature oöcytes squirted through the incision into the alcohol surrounding the specimen.

The Reproductive System

Upon opening the queen, even in the contracted condition, one is immediately impressed by the relatively great size of the reproductive system. All the other organs occupy less than half the haemocoelar space, the organs of reproduction requiring the rest of it. The ovaries are largest and

most conspicuous but the spermatheca and its duct are likewise remarkable, the first two for their size and the last for its length and convolutions (fig. 2).

THE VAGINA AND THE MEDIAN OVIDUCT: A rather wide, slit-like, ex-

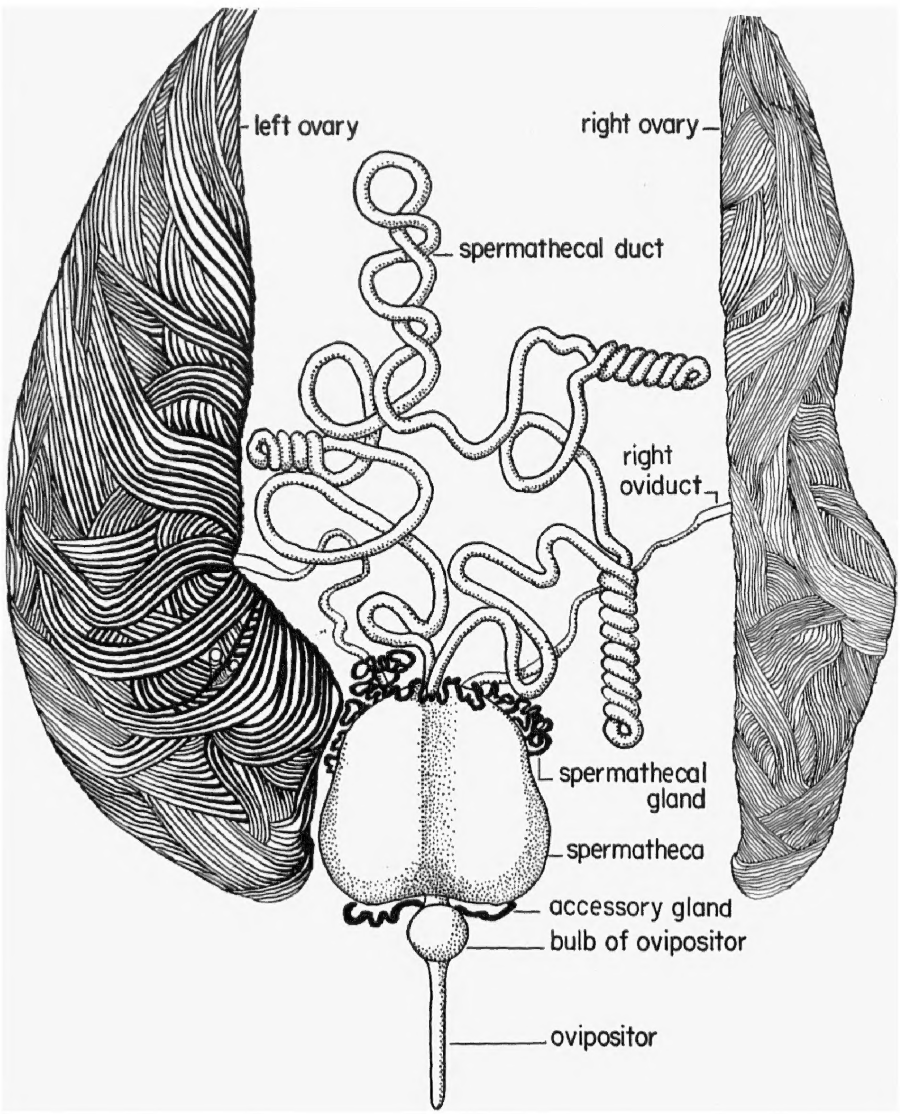

FIG. 2. Reproductive system of *E. burchelli* queen ('49 VB-I). The left ovary has been turned to expose the median aspect; the right ovary in dorsal view. Both are moved from the midline to reveal other parts. The median oviduct and vagina lie beneath the spermatheca and the proximal end of its duct. The ovaries are enlarged only half of the magnification given all other parts.

ternal common opening leads into the vagina on the dorsal wall of which the spermathecal duct arises almost immediately. The vagina narrows somewhat and then broadens gradually to join the median oviduct. No anatomical separation of the two is possible.

The median oviduct is quite elongate and extends forward beneath the spermathecal duct to the anterior end of the spermatheca. Generally it is a rather large, tubular organ quite unlike the saccular shape in the species illustrated by Holliday (1904). During the short time it is distended with oöcytes, however, it is very much larger and sac-like. It is always a rather translucent and delicate structure, compared with the robust spermathecal duct above it, but when distended with oöcytes it appears to be also quite fragile. The two oviducts join its anterior end at an acute angle and close together. They do not approach it laterally as shown for *E. schmitti*. At their junction the median oviduct is only slightly larger in diameter than the paired oviduct.

THE PAIRED OVIDUCT: Within the ovary the oviduct is greatly expanded into a calyx in order to accommodate all the ovarioles communicating with it. It must also be voluminous to receive the vast numbers of oöcytes discharged into it simultaneously from the follicles. Upon leaving the ovary, the oviduct is, at first, quite wide but flattened so that it equals about one-fourth to one-sixth of the width of the calyx. It then narrows gradually into a very slender tube not more than about one-tenth of the width of the calyx. This small diameter is maintained for about one-third of its length after leaving the ovary. Its general direction is posterior along the ventral part of the haemocoele, but its course is erratic, with one to three complete reversals in direction for short distances. As the oviduct nears the spermathecal region it gradually increases in size again to become a rather large tube roughly five times its preceding diameter.

The posterior half, or slightly more, of the length of the oviduct possesses many minor turns or bends in its course. It approaches the midline and joins the median oviduct beneath the spermatheca. It is probable that the oviduct acts as a reservoir for the temporary storage of oöcytes during oviposition as already suggested in the mention of the physogastric queen. In figure 2 the ovaries, having been drawn away from the median area, of course show these ducts as more or less straightened out to preserve their true approximate length.

THE OVARY: The ovary is always very large but becomes enormous just prior to egg deposition. It is smallest of course in a virgin queen and in the fully contracted, functional queen near the end of the statary phase when all of the mature oöcytes have been released into the oviducts or deposited. The ovaries have flat median surfaces where the two are firmly pressed together in the haemocoelar midline. The outer, or lateral, margin

of an ovary is somewhat irregular owing to the grouping of ovarioles, to their twisting and folding in the ovary, and perhaps to the pressure of other organs. The posterior end partially encloses the lateral and dorsal surfaces of the spermatheca and is somewhat wider than the anterior end. The anterior end slopes gently downward and from the lateral border towards the midline. This is due to the fact that each ovariole tapers distally until only the terminal filaments are present. The ovary extends forward into the second segment of the gaster and, when filled with oöcytes, may also occupy the first segment. The terminal filaments always reach to the first segment of the gaster and, in an old female, some seem to penetrate the cavity of the petiole.

The ventral surface of an ovary is slightly concave, especially at a point slightly posterior to its center where the paired oviduct connects with it. When viewed from either the lateral or the dorsal aspect it is quite apparent that the tapering ends of the ovarioles are grouped in clusters, each of which is intertwined with other similar masses, giving the impression that such clusters have been roughly braided. A large tracheal branch penetrates the middle of the ovary, and its lesser branches and tracheoles ramify between the ovarioles.

The number of ovarioles in the ovary of a mature female has always been a matter of interest to entomologists, and almost invariably the total has been recorded for each species studied. It is also of interest because the number sometimes is less than in the immature stadia. Further, in cases where the ovarioles are fairly numerous it has been discovered that there is considerable individual variation in the exact number present. In ants it has been observed, too, that workers suffer a reduction in their numbers as compared with the queen. It has been estimated that the average number of ovarioles for all species of insects may be about six or eight to the ovary.

To determine the number of ovarioles in *E. hamatum* or in *E. burchelli* proved to be very difficult; in fact, only an approximate number can be given here, but it is thought to be fairly accurate. A first attempt was made to count the number from serial sections of the ovary. This was abandoned because of the difficulty in keeping track of so many ovarioles in a large number of succeeding sections and because more anteriorly situated ovarioles continued to appear in later sections. Also, nearly all of the ovarioles are reflexed somewhat so any one may appear more than once in a section. The average number of fully exposed ovarioles on the median lateral surface of the ovary was 54. In an arbitrarily selected narrow strip across the ovary, the counts varied from 25 to 50 ovarioles. Thus the number of ovarioles in depth from side to side of the ovary

fluctuated so greatly in different portions of the ovary that this method of estimating the total proved unsatisfactory.

Finally, with the help of a colleague, Prof. Asher E. Treat, an ovary of *E. burchelli* ('48 VB–I; Schneirla and Brown, 1950) was anchored in alcohol to the substratum and the ovarioles were dissected singly from the ovary. The number was recorded exactly as the work progressed. Dissection was made with the aid of two slightly hooked, very fine needles which, even so, were thicker than the diameter of each ovariole removed. The ovarioles were broken near their bases one at a time, so far as possible, and the vitellarium was entirely removed to the germarium or to the terminal filament. Where more than a single ovariole was removed the number was determined before we proceeded with further dissection. The total count of ovarioles taken from the ovary was 1149 actually dissected and isolated. Even in this case it is estimated that perhaps an error of 15 per cent occurred because of ovarioles damaged and lost during dissection. It is quite safe and conservative to assume there are at least 1200 ovarioles in an ovary, and the actual number is probably nearer 1300 in a single ovary of this species.[1]

During the dissection of the ovariole a few additional observations were made. First, it was noticed that some ovarioles left their point of basal attachment and continued away for some distance almost in a straight line. Others curved away gently and still others were immediately bent at sharp angles from their point of origin. Second, a few ovarioles had fewer than the normal number of developing oöcytes in the vitellarium and showed clear spaces where oöcytes should have been. These were seen and identified before an effort was made to dissect them. Third, 11 ovarioles were completely empty, and no contents seemed to be present even in the germaria.

The ovariole is very slender and exceedingly long. Its taper in a contracted queen is quite regular and so gradual as to be scarcely noticed until it is dissected and mounted entire. There is no evident external diminution in size where it passes over into the terminal filament. The latter is also unusually long and tapers slowly to a fine thread-like tip. No suspensory ligament was discovered, and the attenuated ends seem to lie free or to be very lightly anchored in the ventral and dorsal fat bodies.

[1] While Schneirla has accepted and cited the number of ovarioles from the above count in advance of the publication of this paper, one such citation may be confusing and should be corrected at this opportunity. Schneirla (*in* Schneirla and Brown, 1952, p. 27, footnote) mentions that 1200 ovarioles were found. The number reported refers to one ovary, not both ovaries.

The ovarioles arise from all sides of the calyx at the upper end of the paired oviduct, and their first direction is normally outward at right angles to the basal point of attachment. Very shortly, however, they generally turn dorsally and forward or are bent as previously mentioned. The apical ovarioles continue their course anteriorly with slight or no bends in them. They are all interwoven in small groups or clusters of about 50 or more, which makes it difficult to count them or to dissect one out entire. Details concerning their actual attachment and course will be supplemented in a later paper on the histology.

THE SPERMATHECAL DUCT: Originating on the dorsal wall of the vagina, almost immediately above the latter's external opening, the spermathecal duct runs anteriorly over the median oviduct. At its origin the duct is as wide as the vagina and lies close to it and the oviduct throughout the length of these parts of the reproductive system. At this place it is rather ovate or flattened, but near the anterior end of the spermatheca it becomes rounded and continues this shape for the rest of its length.

The duct is remarkable in two respects: first, it is exceedingly long, perhaps longer than the gaster itself; second, it possesses several very tight coils, usually from three to six in number. Its anterior portion is looped and coiled just above the ventral fat body tissue, but it apparently never invades the latter. Its twists and coils are peculiar to the individual queen, and their positions in the haemocoele and the general course of the duct itself seem never to be exactly duplicated in another female. Often it extends into the second segment of the gaster.

Eventually the spermathecal duct turns posteriorly and joins the spermatheca on the latter's anterodorsal surface. While the duct is a large, conspicuous organ, its diameter anteriorly never exceeds that of the median oviduct or that of the lower end of the paired oviduct.

THE SPERMATHECA: This organ is very large and roughly heart-shaped. Along the upper surface is a shallow depression in the median line which is most accentuated along the posterodorsal and upper posterior margins of the spermatheca. In this concave depression the hind intestine pursues its course towards the rectal area, making a sharp bend ventrally as it passes back over the spermatheca.

The spermatheca is collapsed, almost flat, and slightly folded in a virgin queen but is turgid and ovate in cross section when filled with sperm. Its enormous relative size and capacity confirm the evident significance of the organ in the sexual behavior of the queen. It is no doubt closely related to the long reproductive life and great biotic potential of the female in her production of several (about 10) prodigious broods an-

nually (Schneirla, 1949). Regardless of the possibly different ages of the fertile queens examined, the spermatheca invariably appeared very large and distended.

Spermathecal Glands: A pair of very irregularly twisted, simple tubular glands are attached to the spermatheca directly above the junction between this organ and the spermathecal duct. They may, or may not, pass posteriorly over the dorsal surface of the spermatheca at first. In both cases they turn ventrally rather quickly, on either side of the spermathecal duct, towards the ventral fat body which may partially cover a portion of them, especially in the physogastric female.

These glands are much twisted and looped but do not form the tight coils characteristic of the spermathecal duct. Most of their length lies beneath the spermatheca, but occasionally their terminal portions may ramify farther forward in the body. They are rather slender glands as compared with their length.

The Accessory Glands: A pair of glands arises anterior to the basal bulb of the ovipositor. The shorter of the pair is also the larger in diameter. The homologue, while more slender, extends beneath the ventral, posterior surface of the spermatheca. The latter is much more erratic and sinuous in its course than its mate. It also appears to possess a slightly more irregular outline owing to numerous, very small swellings that can be seen on its surface. These glands are, no doubt, the homologues of the colleterial and poison glands of other insects and may have the latter's functions in the army-ant queen. If so the right gland, according to Snodgrass (1933), is the poison gland opening into the channel of the sting, while the left one may be for other purposes, possibly for lubrication. It opens anterior to the base of the sting. The latter is the shorter and larger one in the army-ant queen.

Measurement of the Organs: As can be seen from figure 2, it would be quite difficult to measure accurately the lengths of the ducts of the reproductive system, for they are so tortuous in their course through the gaster. Nevertheless an attempt was made to provide these data by following them with the ocular micrometer. The dissected reproductive system of a *burchelli* queen ('48 VB–I; Schneirla and Brown, 1950) was used for all details shown below, except for the spermathecal duct which proved to be less subject to extensive error when measured in a *hamatum* queen ('48 H–D; Schneirla and Brown, 1950) where it chanced to be better exposed. It should be noted that the ovary of the *burchelli* queen used here is approaching the physogastric condition. Other ovarial measures will be published in part 3 of these papers. All dimensions are in millimeters.

Vagina and median oviduct: length, 2.6; base width, 0.34; distal width, 0.26
Paired oviduct: length, 4.52; base width, 0.217; middle width, 0.17; near calyx, 0.22 × 0.65
Ovary: length, 10.18; breadth, 2.17; depth, posterior, 3.74; at oviduct, 2.17; anterior at germaria, 2.69
Spermathecal duct: length, 17.22; width, 0.16
Spermatheca: length, 2.87; width, 2.6; depth, 1.74
Spermathecal gland: width, 0.13
Bulb of ovipositor: length, 1.48; width, 1.40
Ovipositor: length, 1.60

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